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Protected areas act as a buffer against detrimental effects of climate change – evidence from large-scale, long-term abundance data

Running head: Protected areas buffer against climate change

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Abstract

Climate change is driving species to shift their distributions towards high altitudes and latitudes, while habitat loss and fragmentation may hamper species ability to follow their climatic envelope. These two drivers of change may act in synergy, with particularly disastrous impacts on biodiversity. Protected areas, PAs, may thus represent crucial buffers against the compounded effects of climate change and habitat loss. However, large-scale studies assessing the performance of PAs as such buffers remain scarce and are largely based on species occurrence data. Conversely, abundance data have proven to be more reliable for addressing changes in wildlife populations under climate change. We evaluated changes in bird abundance from the 1970s–80s to the 2000s inside and outside PAs at the trailing range edge of 30 northern bird species and at the leading range edge of 70 southern species. Abundances of retracting northern species were higher and declined less inside PAs at their trailing range edge. The positive effect of PAs on bird abundances was particularly marked in northern species that rely strongly on PAs, i.e. their density distribution is largely confined within PAs. These species were nearly absent outside protected areas in the 2000s. The abundances of southern species were in general lower inside PAs and increased less from the 70s–80s to 2000s. Nonetheless, species with high reliance on PAs had much higher abundances inside than outside PAs in the 2000s. These results show that PAs are essential in mitigating the retraction of northern species, but also facilitate northward expansions of southern species highly reliant on PAs. Our study provides empirical evidence documenting the role of PAs in facilitating species to adjust to rapidly changing climatic conditions, thereby contributing to the mitigation of impending biodiversity loss. PAs may thus allow time for initiating wider conservation programs on currently unprotected land.

43 Introduction

44

45 Anthropogenic climate change has influenced all the ecosystems on Earth (Scheffers *et al.*,
46 2016) and is projected to reduce global biodiversity remarkably (Bellard *et al.*, 2012). Climate
47 change is shifting climatic conditions of species and ecosystems towards higher latitudes and
48 altitudes and species are tracking these changing conditions by shifting their distributions
49 (Chen *et al.*, 2011). However, habitat loss and fragmentation driven by anthropogenic land
50 use may impede the ability of species to follow their climatic envelopes (Robillard *et al.*,
51 2015). Indeed, the joint effects of climate change and habitat loss are expected to be
52 disastrous for biodiversity (Oliver *et al.*, 2017, Travis, 2003). Species inhabiting high latitudes
53 and high altitudes may be particularly exposed to the consequences of climate change because
54 they may run out of space into which they can retreat, leading to increased extinction risk
55 (Pacifici *et al.*, 2017). This effect may further be compounded if the arctic and boreal biomes
56 at high latitudes warm up at a higher rate than regions at lower latitudes (IPCC, 2013).
57 Evidence is mounting that this may indeed be the case, since boreal and montane species in
58 northern Europe have shifted their distributions faster than southern species (Virkkala &
59 Lehikoinen, 2014), and exhibit rapidly decreasing populations (Lehikoinen *et al.*, 2014, Post
60 *et al.*, 2009).

61 Protected areas (hereafter PAs) are among the most important means for preserving habitats
62 and ensuring species persistence (Watson *et al.*, 2014). Yet their role in mitigating the impacts
63 of climate change has been questioned (Monzón *et al.*, 2011). The main limitations of the
64 current PA network for ensuring nature protection under dynamic and asymmetrical climate
65 change are the static nature of the network, the spatial bias and low coverage (Monzón *et al.*,
66 2011). These shortcomings relate to species moving outside the network of PAs under shifting

climatic conditions (Hannah *et al.*, 2007). There is however evidence that PAs are important for conserving rare species and for the overall maintenance of biodiversity under climate change (Thomas & Gillingham, 2015). PAs have also been found to facilitate species range expansions (Thomas *et al.*, 2012), and are suggested to help species to persist on trailing edges of contracting or moving distributions (Gillingham *et al.*, 2015b). However, the evidence for this is restricted to narrow geographical areas and very few habitats. Understanding the ecological, physiological, genetic and biogeographical mechanisms underpinning species range shifts is fundamental for designing effective conservation strategies and adaptations to climate change (Bonebrake *et al.*, 2018)

Most findings concerning changes in species distributions under climate change are based on occurrence data, and although abundance data are limited for many taxa globally, recent evidence shows the increased reliability in generating outcomes for conservation prioritization when abundance data are used (Howard *et al.*, 2014, Johnston *et al.*, 2015). Moreover, many studies have concentrated on projecting future impacts, however attention is also required on studying the current impacts of climate change on species, and for validating and improving projections of future impacts (Pacifici *et al.*, 2017). There is thus a need for studies using large-scale long-term abundance data of wide taxonomic breadth for studying past and present impacts of climate change on species distributions.

To heed this call, we studied the impact of PAs in aiding the expansion of populations of southern species and in maintaining the densities of retracting populations of northern species under climate change. To achieve this, we used nation-wide Finnish land bird density data from two time periods, namely 1970–1989 and 2000–2014, available from within and outside PAs. We evaluated factors affecting bird abundances in the two periods separately for the leading (i.e. northern) range edge of 70 southern species and for the trailing (i.e. southern) range edge of 30 northern species (Fig. 1; Table S1).

Based on previous studies conducted using occurrence data (Gillingham *et al.*, 2015b, Hannah *et al.*, 2007, Monzón *et al.*, 2011, Thomas *et al.*, 2012, Watson *et al.*, 2014), we hypothesize that abundance changes between the two time periods at both trailing and leading range edges are more positive inside PAs than outside. This means that (i) abundances of northern species, the ranges of which are retracting toward the north, will have declined less inside protected areas than outside on the trailing range edge. In addition, we expect that (ii) on the leading range edge of southern species the abundance increases would be greater inside protected areas than outside. However, since species differ in their reliance on PAs we hypothesize the presence of an interaction between PA reliance and protection status of a given site (protected or unprotected), especially since species less reliant on protection may thrive also outside PAs (Fraixedas *et al.*, 2015). The effect of protection is therefore predicted to be stronger for species highly reliant on site protection, whereas species less reliant to PAs, e.g. farmland birds in Finland, exhibit a weaker response to site protection.

Materials & methods

Line transect data

We used Finnish land bird line transect data spanning a period from the early 1970s to the present day (Virkkala & Lehikoinen, 2014). Transects were 3–6 kilometers long and their locations were pre-set. Transects were surveyed once a year by foot, walking at an average speed of 1 km / 45 min. The survey period was between the 21st of May and the 20th of June in South-Finland and between the 10th and the 30th of June in North-Finland. In montane areas, the surveying continued until the 5th of July. Each transect was surveyed in the early morning under favorable conditions for detection of birds, and all observed bird individuals were counted. For each observation, the state and behavior of the bird was recorded (singing,

calling, flying, sex, age, nest, brood and flock-size) as detailed as possible. Based on this information, all observations were transformed into pairs, which is the census unit (Virkkala & Lehikoinen, 2014). A single individual was always counted as one pair as was a nest and a brood. For flocks of adult birds, the number of individuals was divided by two for transformation into pairs. If the sexes were distinguishable in a flock of adult birds the number of individuals of the more abundant sex was used as the number of pairs. For flocks of early breeding passerines, where age and sex could not be identified, the number of individuals were divided by five for transformation into pairs, because flocks may include broods. Thus, the unit of abundance for each species was the number of pairs for censused amount of kilometers. This methodology is appropriate to obtain robust relative abundances of species over large areas (Järvinen & Väisänen, 1975, Lehikoinen & Virkkala, 2016).

Each transect was classified according to its i) protection status; falling either inside or outside PAs, and ii) time period; either 70s–80s or 2000s according to the year of survey of either 1970–1989 or 2000–2014, respectively (Santangeli *et al.*, 2017). All monitored PAs belonged to IUCN protected area categories I-IV (Dudley, 2008). The time of PA establishment is of low importance for the purpose of this study because PAs are typically established in pristine or relatively good quality habitats, such as old-growth forests, unditched forest mires or large and wet open mires that have been in a similar state for several decades. Therefore, even the most recently established PAs are comparable in terms of habitat quality with the PAs established decades ago. Transects running across PA boundaries were excluded to avoid edge effects (Santangeli *et al.*, 2017). To account for spatial changes in densities between the two time periods (see above), we divided the country into 100 km x 100 km squares (hereafter squares) following the Finnish national uniform coordinate system. This resolution represents an optimal tradeoff between the need to retain variation in the data at high enough resolution to depict spatial patterns in abundance, while at the same time

allowing large enough sample sizes within each square in the different periods (the same methodology in Santangeli *et al.*, 2017). Only squares that had line transect data from both periods and both protection statuses were included in the study. This resulted in 40 squares with sufficient line transect data and broad spatial coverage throughout the country (Santangeli et al., 2017; Fig. 1).

Definition of range edges and species-specific measures

We studied 128 species of land birds having at least 20 observations during both periods (Lehikoinen & Virkkala, 2016). Each of the species studied were classified as either southern or northern species based on their density distribution in the 70s–80s (Lehikoinen & Virkkala, 2016). This period was chosen for edge definition as it is the starting point for studying the population density changes between the time periods of the study. Since the observed population changes in North Europe have been in line with predictions based on climatic suitability (Jiguet *et al.*, 2013, Virkkala *et al.*, 2014a), we contend that the witnessed abundance changes in the defined range edges could be driven mainly by climate change. This contention may be especially true inside PAs, where habitat quality has remained unaltered (Virkkala & Rajasärkkä, 2011).

A species was classified as southern if its central gravity of density (introduced in (Lehikoinen & Virkkala, 2016)) was situated in the southern half of the country and if the species distribution exhibited a northern edge within the country (i.e. zero density at least in the northernmost latitudinal row of squares). Conversely, a species was classified as northern if its central gravity of density was situated in the northern half of the country and if the species distribution exhibited a southern edge within the country. This yielded a total of 70 southern and 30 northern species (Table S1). 28 of the 128 species studied did not fulfill

either of these criteria, because they occurred throughout the country, and were thereby excluded from the study.

The range edges of southern and northern species were defined using a percentage of the cumulative density sums in the first period, using data from both inside and outside PAs (Fig. 1). To do this, we summed the densities of all squares in latitudinal rows of squares (hereafter rows) and used the cumulative density sums of these rows, starting from the southernmost row on southern species and northernmost row on northern species. For northern species, the trailing (i.e. southern) range edge of the distribution was defined as starting from the row where the cumulative density sum of the species in question reached at least 95% of the total density of the species and ending at the southernmost row (Fig. 1). For southern species, the leading (i.e. northern) range edge was defined as starting from the row where the cumulative density sum of the species in question reached at least 95% of the total density of the species. The range edge was defined as ending at the northernmost row (Fig. 1).

We calculated a PA reliance index, hereafter PA reliance, for each species by dividing the mean density within PAs by the overall mean density of that species in Finland. In this calculation we included both time periods but excluded the range edges to avoid circularity. The PA reliance ranged from 1 to 0 where the extreme values corresponded to all and none of the densities of the species being observed inside PAs, respectively. The PA reliance gives a rough estimate of the importance of PAs for the specific bird species. Thus, PA reliance was used to explore the relevance of PAs for the distribution changes of each species in the study. Because PA reliance is most certainly affected by habitat preferences, species were also divided into four categories based on the dominant habitat in which they are found: 1. farmland-urban, 2. forest, 3. wetlands (including rocky outcrops and peatlands) and 4. montane (Lehikoinen & Virkkala 2016).

Protected areas in Finland

Approximately 78% of the Finnish land area is forested (EEA 2015) and only 12% of the forested land is protected, whereas forestry is operated in the rest of the area (Natural Resource Institute Finland, 2016). Logging is prohibited in protected areas and they typically support older and more layered forest, as well as higher volumes of dead wood as compared to unprotected forest lands (Metsähallitus, 2018). Peatlands cover 28% of the Finnish land area, out of which 19% are open mires and 81% forest mires. Of the original peatland area c. 60 % has been drained by ditching for forestry purposes (Fraixedas *et al.*, 2017), resulting in pristine forest mires being rare outside PAs. Only 13% of the Finnish peatlands are protected. These peatland PAs consist of pristine or relatively good quality habitats including large open mires and the unditched forest mires surrounding them. PAs have also been established to protect threatened habitats including traditional rural habitats, coastal habitats and inland shore meadows (Raunio *et al.*, 2008). In general, major land use actions that could damage nature are strictly prohibited inside PAs. In most PAs recreational activities, e.g. berry and mushroom picking and hiking are allowed, while limitations on camping, hunting, use of motor vehicles as well as access to especially sensitive bird nesting areas are in place in many PAs (Metsähallitus, 2018).

Statistical analyses

To study density changes at the distribution edges we used generalized linear mixed models (GLMM) separately for southern and northern bird species. The response variable in the models was the observed number of pairs in a given square, period (70s–80s vs 2000s) and protection status (within vs outside PAs). The sample sizes for each species per period and protection status are shown in Table S1. The total sample size for the analysis on northern

213 species was 964, i.e. 241 unique species by square sample units for each combination of
214 period and status. The total sample size for southern species was 3212, consisting of 803
215 unique species by square sample units.

216 Squares where a single species was not observed on either of the protection statuses and either
217 of the periods were removed from the dataset. This was done to reduce the number of zeros in
218 the dataset. The species-specific number of squares with data on both periods and protection
219 statuses are presented in Table S1. Despite removing the squares with no observations, the
220 datasets on both northern and southern species contained marked amounts of cases with zero
221 pairs observed. 46.1% and 41.1% of all cases represented zero pairs observed for datasets on
222 northern and southern species, respectively. The residuals of GLMMs with a logarithmic link-
223 function and Poisson distribution showed considerable overdispersion, as depicted by the ratio
224 of Pearson residual deviance to degrees of freedom: 5.91 and 6.91 for models describing
225 northern and southern species, respectively. Since Pearson residuals did not show any
226 systematic patterns against all covariates (Zuur *et al.*, 2009), GLMMs with negative binomial
227 distribution (function glmmadmb in R (Fournier *et al.*, 2012)) were used to account for the
228 observed overdispersion.

229 The period was used as an explanatory factor to assess the changes in abundances between
230 70s–80s and 2000s. To assess the effect of protection status and species reliance on PAs,
231 protection status and standardized and centered PA reliance were used as explanatory
232 variables. To account for decreasing abundances towards higher latitudes and longitudes,
233 standardized and centered mean latitude and mean longitude of the squares were set as
234 explanatory variables. Square and protection status specific log-transformed total transect line
235 length was used as an offset in the model, in order to account for sampling effort (see
236 Santangeli *et al.*, 2017). This is important because neglecting sampling effort can cause biases
237 in the analyses especially when presence-absence data are used (Kujala *et al.*, 2013).

Transects in PAs covered a total of 3590 kilometers in the first and 10330 kilometers in the second period. Transects outside PAs totaled 5119 kilometers in the first and 9521 kilometers in the second period. In the models, log-transformed total length of the transect lines, latitude, longitude and protected area reliance were continuous variables, the response variable was an integer and protection status and period categorical variables. No strong correlations were detected among the explanatory variables; all Pearson correlation coefficients were below 0.5 (Booth *et al.*, 1994).

We built competing models to investigate which explanatory variables had the largest impact on abundances. We included mean latitude and longitude of the squares and period to all the models except the simplest intercept-only model. In addition to these fixed explanatory variables the competing models consisted of all the possible subsets of explanatory variables and interactions between period, protection status and PA reliance. Thus, the most complex model contained the main effect of latitude, longitude, protected area reliance, protection status and period as well as all two-way interactions and the three-way interaction between protected area reliance, protection status and period.

In all models, we included square and species identity as crossed random factors to account for the lack of independence and potential pseudoreplication arising from repeated observations within squares and species. In order to account for the fact that species vary in their densities between PAs and non-PAs, the PA status of the transect was included as random slope in the models that included the main effect of PA status. Species with close phylogenetic relations are more likely similar in their responses to climate change than distant species. We accounted for these phylogenetic relationships in the analysis by running three models identical to the most complex competing model (described above) and adding three different levels of phylogenetic grouping. These three models were ranked using AICc values only (Akaike, 1974, Sugiura, 1978) and the level of phylogeny in the model with lowest AICc

value was chosen for all the competing models. The phylogenetic grouping levels were: species alone, species nested within family and species nested within order. The taxonomy used followed that of IOC World Bird List (Gill & Donsker, 2018). For both northern and southern species the model with species alone had the lowest AICc values (Tables S2 & S3). Therefore, these phylogenetic levels were used in all of the competing models. Square, species and family were categorical variables in the models.

Because PA reliance may be driven by habitat use, we also included competing models where PA reliance was replaced with a habitat class variable. Finally, the 26 competing models were evaluated according to their AICc values for both northern and southern species (Tables S4 & S5). The model with the lowest AICc value was chosen as the best to explain bird densities at the distribution edges. However, if several models were ranked with $\Delta AICc \leq 2$, we first investigated whether the top ranked model was more parsimonious than the other models within $\Delta AICc \leq 2$ (i.e. the other models included more uninformative parameters where the 85% confidence interval included zero; (Arnold, 2010)). If the top ranked model was less parsimonious, we proceeded with multimodel inference and model averaging (using the R package MuMin (Bartón, 2018)) over the top-ranked models showing no uninformative parameters.

The residuals of both models used for explaining abundance of northern and southern bird species on range edges were inspected for the presence of potential spatial autocorrelation, and that of unexplained patterns (Zuur *et al.*, 2009), but none were detected. All statistical analyses were performed with R software version 3.4.4 (R Core Development Team, 2017).

287 Results

288 For northern species three top ranked models exhibited differences in AICc-values of less
289 than two units (Table S4). The third ranked model contained the uninformative parameter for
290 the three-way interaction between period, PA reliance and PA status. The 85% confidence
291 interval for this parameter ranged from -0.11 to 0.47 (NBGLMM: 0.18 ± 0.20, z=-0.89,
292 p=0.37). Model averaging was therefore conducted using the two AICc top-ranked models
293 that did not contain uninformative parameters. This revealed that the parameter for the
294 interaction between period and protected area reliance, present in the top-ranked model, was
295 uninformative (85% CI: -0.29–0.05; NBGLMM: -0.12 ± 0.12, z=-0.98, p=0.33). For inference
296 regarding northern species we therefore chose the simplest, second-ranked model. This model
297 contained the following variables: latitude, longitude, period, protection status, protected area
298 reliance, the interaction between period and protection status and that between protection
299 status and protected area reliance (Tables 1 & S6).

300 Abundances of northern species on their trailing range edge were higher inside PAs (Table 1).
301 Bird abundances decreased with increasing protected area reliance, but an interaction between
302 protection status and PA reliance indicated that the decrease was much less steep inside PAs
303 than outside (Fig. 2a). Moreover abundances of northern species on their trailing range edge
304 declined from the 1970s–80s to the 2000s, and an interaction between protection status and
305 period showed that the change was less negative inside PAs than outside (Fig. 2b).

306 For southern species, two top AICc-value ranked models exhibited an AICc difference of less
307 than two units (Table S5). The second-ranked model contained one uninformative parameter
308 more than the top-ranked model. This parameter, the three-way interaction between period,
309 protections status and protected area reliance, was uninformative (85% CI: -0.15–0.17;
310 NBGLMM: 0.01 ± 0.11, z=0.08, p=0.94). Thus the simpler, top-ranked model was used for

311 inference for southern species. This model included the following variables: latitude,
312 longitude, period, protection status, protected area reliance and the interactions between
313 period and protection status, between protection status and protected area reliance and
314 between period and protected area reliance (Tables 2 & S7).

315 Southern species on their leading range edge were less abundant inside than outside PAs
316 (Table 2). Protection status however exhibited interactions with PA reliance and period.
317 Inside PAs bird abundances increased markedly with increasing PA reliance (Fig. 2c),
318 whereas they were not affected by PA reliance outside of PAs (Table 2). However, PA
319 reliance interacted positively with time period, showing that bird abundances increased with
320 increasing PA reliance from the 1970s–80s to the 2000s (Fig. 2d). Abundances of southern
321 species on their leading range edge showed an overall increase from the 1970s–80s to the
322 2000s (Fig. 2d). The interaction between protection status and period showed that this
323 increase was not as marked inside PAs as outside (Table 2, Fig. 2d).

324

325 Discussion

326 The results show that the abundances of northern species at their trailing range edges have
327 declined less inside than outside protected areas, with the abundances of especially species
328 with high PA reliance remaining higher inside than outside PAs. While the latter finding may
329 was partly expected due to generally higher reliance on PAs among northern species (mean
330 PA reliance 0.63 ± 0.14 SD), it underlines the fact that species with the highest reliance on
331 protection were nearly absent outside PAs in the 2000s. This may be explained by the high
332 proportion of old-growth boreal forests in the Finnish protected areas which has been shown
333 to have positive effects on the specialization of the avian community (Häkkilä *et al.*, 2017).
334 Our findings therefore emphasize the importance of PAs in mitigating declines of boreal bird

335 species under climate change. This result is particularly relevant in light of climate change in
336 the boreal biome being predicted to be much more rapid than that in other regions, carrying
337 serious consequences for ecosystems and associated wildlife (Loarie *et al.*, 2009). Despite the
338 fact that northern PAs are experiencing among the most rapid rates of climate change (Loarie
339 *et al.*, 2009) they are able to slow down the retraction of species ranges, albeit not fully
340 prevent it. Our results add to the accumulating evidence underscoring the importance of PAs
341 which have previously been shown to aid persistence of northern species at temperate region
342 by studying occurrences (Gillingham et al., 2015a) and to facilitate the adaptation of northern
343 species to temperature changes (Gaüzère *et al.*, 2016), as well as support more cold-dwelling
344 bird communities (Santangeli *et al.*, 2017) by investigating changes in the thermal signature
345 of bird communities (Devictor *et al.*, 2008). The findings suggest that PAs serve as refuge for
346 northern species of which many are boreal biome specialist facing high pressure from a
347 rapidly warming climate (Loarie *et al.*, 2009, Pacifici *et al.*, 2017). The findings are also in
348 line with earlier results showing that the probability of occurrence among northern species
349 increased with increasing cover of protected area in a 10 km x 10 km atlas square (Virkkala *et*
350 *al.*, 2014b). However, that study did not separate surveys conducted inside and outside PAs,
351 and used presence-absence data without correcting for observation effort. In contrast, our
352 study explicitly accounted for varying survey effort and has thus been able to reveal
353 significant changes in bird abundances.

354 Our findings regarding southern species show that abundances at the leading range edge were
355 higher and increased more outside than inside PAs from the 1970s–80s to the 2000s, which
356 contradicts our initial hypotheses. The average reliance on protected areas was low in
357 southern species (mean protected area reliance (0.39 ± 0.19 SD), and the under-representation
358 of species strongly reliant on PAs in the south may be an explanation for the lack of
359 relationship between PA reliance and abundance outside PAs in the 70s–80s. However,

360 species that are highly reliant on PAs exhibited markedly higher densities inside PAs than
361 outside (Fig. 2d). This suggests that PAs are important for expanding populations of southern
362 species with high PA reliance; a conclusion also reached by studies based on occurrence data
363 on birds and butterflies (Gillingham *et al.*, 2015b) and abundance categories on odonates and
364 butterflies (Gillingham *et al.*, 2015a). Species with a high reliance on PAs may use PAs as
365 stepping stones when moving into new areas (Hiley *et al.*, 2013). However increasing PA
366 reliance affected abundances positively also outside PAs in the 2000s compared to the 70–
367 80s. This may be the result of PA designation being biased towards boreal habitats. Thus,
368 species with high PA reliance are boreal biome specialists, which may find more suitable
369 habitat outside PAs when expanding their distributions from the temperate zone into the
370 boreal zone. This result underscores a striking challenge for national conservation policy
371 posed by climate change, where the managing and expanding of the current PA network in
372 order to maintain habitat for northern species needs to be balanced with maintaining habitat
373 important for the northward expansion of southern species.

374 Our large-scaled long-term study provides quantitative evidence on the performance of PAs
375 under climate change and as the previous studies concentrate to the temperate region (e.g.
376 Gillingham *et al.*, 2015a, Thomas *et al.*, 2012, Watson *et al.*, 2014), widens the current
377 knowledge to cover also boreal region. Besides increasing the geographical coverage of such
378 studies to include one of the regions with highest velocities of climate change (Loarie *et al.*,
379 2009), the large-scaled abundance data increases the reliability of our current view of the
380 positive effects of PAs on range shifts under climate change (Howard *et al.*, 2014, Johnston *et*
381 *al.*, 2015). We must stress that the exact transect locations in this study have not necessarily
382 been the same between the study periods. However, we argue that while this may represent a
383 source of random noise across all the data, it is unlikely that it could bias the results given the

large spatial scale of the sampling units and the wide scale of the whole study where range edges also vary between species.

This long-term documentation of changes in bird abundances shows that PAs play a key role in mitigating the loss of biodiversity under climate change (Johnston *et al.*, 2013), PAs not only facilitate range expansions of species establishing into new areas (Gillingham *et al.*, 2015a, Thomas & Gillingham, 2015, Thomas *et al.*, 2012), but also mitigate the retraction of species shifting under climate change. Moreover, the existing PAs not only mitigate local extinctions of a large number of northern species, but also abundance losses are lower inside PAs compared to outside. Besides facilitating range expansion, PAs contribute to the increase of abundances in already occupied areas of southern species with high reliance on PAs. Climate change may however cause species to be excluded from current PAs due to shifts in climate envelopes (Araújo *et al.*, 2004). Therefore, some PAs may perform poorly in conserving biodiversity under climate change (Araújo *et al.*, 2011), especially given their biased distribution, limited area coverage and variable management effectiveness (Watson *et al.*, 2014). As a result, the future of biodiversity conservation in the long term also strongly relies on efforts put in place on currently unprotected land (Santangeli *et al.*, 2016). While there are international commitments to expand the current PA network (Aichi target 11 in (CBD, 2018, Montesino Pouzols *et al.*, 2014), and implement effective biodiversity conservation actions on unprotected land (Santangeli *et al.*, 2016), they require time and resources, while biodiversity continues to decline at alarming rates. Under this scenario, our results represent an encouraging message for biodiversity conservation. We show that PAs play an important role in mitigating impacts of climate change on biodiversity, providing strongholds for species persistence in the short term, thereby allowing some time for wider protection efforts on unprotected land to start yielding positive effects. Moreover, by buffering against the detrimental effects of climate change, protected areas can buy time

during which the causes of anthropogenic climate change may or may not be remedied. Multidisciplinary work in the field of ecology, conservation and social science should facilitate the implementation of solutions to mitigate the negative impacts of climate change (Bonebrake et al. 2018).

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Table 1. Summary table of the model explaining abundances of northern bird species on their trailing range edges. Significant variables are bolded.

	Estimate	Std. error	z-value	Pr(>|z|)
(Intercept)	**-5.27**	**0.36**	**-14.46**	**<0.001**
Period 2000s	**-0.94**	**0.15**	**-6.31**	**<0.001**
Protected area	**1.43**	**0.21**	**6.81**	**<0.001**
PA reliance	**-0.80**	**0.34**	**-2.34**	**0.02**
Latitude	**1.67**	**0.20**	**8.24**	**<0.001**
Longitude	-0.10	0.10	-1.02	0.31
Period 2000s:Protected area	**0.43**	**0.19**	**2.22**	**0.03**
Protected area:PA reliance	**0.64**	**0.18**	**3.58**	**<0.001**

555 Table 2. Summary table of the model explaining abundances of southern bird species on their leading

556 range edges. Statistically significant variables are bolded.

	Estimate	Std. error	z-value	Pr(>|z|)
(Intercept)	**-4.54**	**0.27**	**-16.62**	**<0.001**
Period 2000s	**0.77**	**0.07**	**11.13**	**<0.001**
Protected area	**-0.57**	**0.11**	**-5.39**	**<0.001**
PA reliance	0.12	0.25	-0.53	0.60
Latitude	**-1.53**	**0.09**	**-16.46**	**<0.001**
Longitude	-0.14	0.09	-1.66	0.10
Period 2000s:Protected area	**-0.33**	**0.10**	**-3.29**	**0.001**
Period 2000s:PA reliance	**0.20**	**0.06**	**3.56**	**<0.001**
Protected area:PA reliance	**1.07**	**0.09**	**11.84**	**<0.001**

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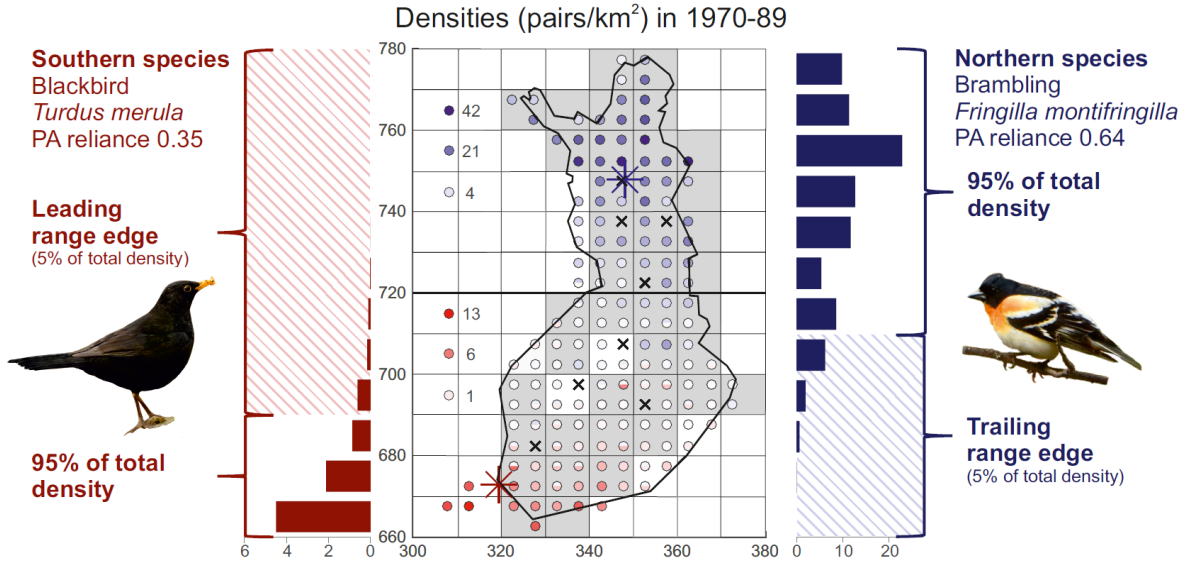

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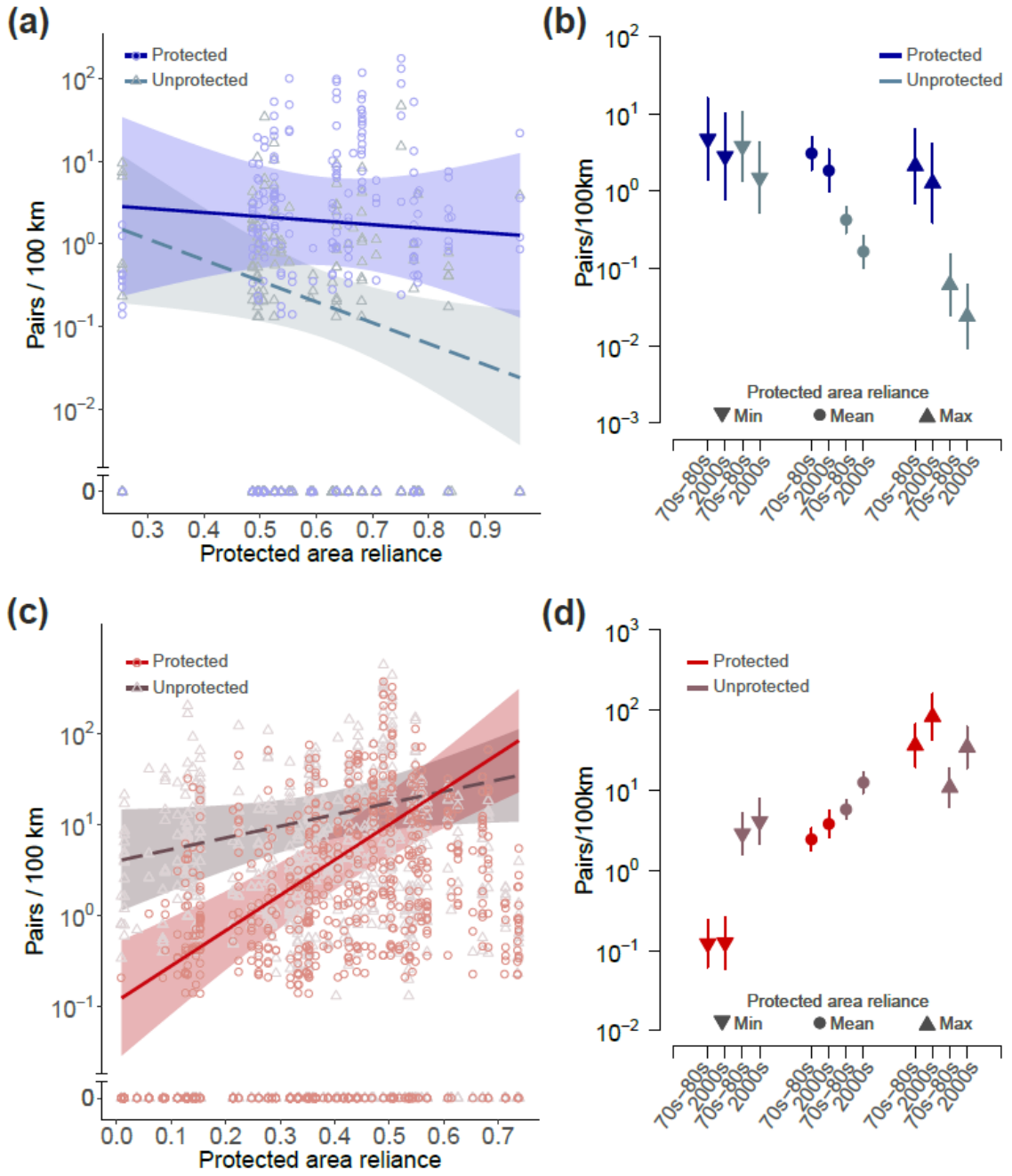
560 **Figure 1. Definition of range edges of southern (red) and northern species (blue)**. Grey
561 squares represent the 100 km x 100 km squares from which abundance data was available for
562 both time periods (1970–89 & 2000–14) and for both protection statuses (protected &
563 unprotected), illustrating the spatial coverage of the data used. Densities of species in 1970–
564 1989 are shown as coloured dots inside each square with a resolution of 50 km x 50 km where
565 the intensity of the colour represents the density as illustrated on the left side of the map.
566 Where the ranges between the northern and southern example species overlap, the density of
567 northern species is represented by the colour in the upper half of the dot and the density of
568 southern species in the bottom half. Asterisks represent the central point of gravity of the
569 densities and black crosses missing data. The histograms on the side of the map represent the
570 sums of abundances in each 100 km wide latitudinal zones of squares. The latitude 720
571 divides the country in half and is, together with the central point of gravity, used to identify
572 species as either southern or northern. The range edges represent the northernmost (on
573 southern species; the blackbird in this example) or southernmost (on northern species; the
574 brambling) 5% of the total density of each species. The range edges for the example species
575 are shown as barred areas.

576



577

578 **Figure 2. Model estimates of bird abundance in response to protected area reliance and**

579 **time period.** Figures **2a,c** show the estimated effects of protected area reliance on bird

580 abundances inside protected areas (solid line) and outside protected areas (dashed line) during

581 the second time period (2000s) of northern species and southern species, respectively; circles

582 represent data points from protected areas and triangles those from unprotected areas. Shaded

583 bands represent the 95% confidence intervals of the effect of protected area reliance on bird

584 abundance. Figure **2b** shows model estimates of the effect of time period on densities of
585 northern species (inside PAs: dark blue, outside PAs: light blue) for minimum (0.25; point-
586 down triangles), mean (0.63; dots) and maximum (0.96; point-up triangles) PA reliances.
587 Figure **2d** shows model estimates of the effect of time period on densities of southern species
588 (inside PAs: red, outside PAs: dark pink) for minimum (0.01; point-down triangles), mean
589 (0.39; dots) and maximum (0.74; point-up triangles) PA reliance indices. The whiskerers in
590 figures **2b,d** represent standard errors of the parameter estimates.

Data availability

Data is deposited in Zenodo (DOI: 10.5281/zenodo.1422373).

Additional information

Supplementary information is available in a separate file.

Competing financial interests

The authors declare no competing financial interests.